Passive Suspension Feeding in a Sea Pen: Effects of Ambient Flow on Volume Flow Rate and Filtering Efficiency

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Abstract. An integrative analysis of passive suspension feeding is developed and tested. It emphasizes the functional role of overall organism design in enhancing the hydromechanic conditions necessary for feeding. Feeding rate, defined as the total number of particles captured per time, is a function of the ambient flow speed which independently affects both the volume flow rate and the filtering efficiency. In the sea pen *Ptilosarcus gurneyi*, volume flow rate initially increases with increasing ambient flow speed, peaks, and then decreases as the animal deforms with the flow. Filtering efficiency, for a given filter geometry, decreases with increasing velocity. However, due to deformation of the filter with flow, higher filtering efficiencies are maintained as a result of the variable porosity filter. Feeding rate is strongly dependent on volume flow rates. The feeding rate initially increases with increasing ambient flow, but then peaks and decreases similar to the volume flow rate. Both volume flow rate and filtering efficiency depend upon the size of the organism and the relative position of the organism in the boundary layer.

Introduction

Aquatic suspension feeding organisms use an array of filtering elements to separate particles from the passing fluid medium. *Passive* suspension feeders rely solely on the relative movement of their filter and the particle-laden water for food capture. In many sessile and benthic organisms, the relative movement is generated by the ambient flow, leaving them highly dependent on the ambient flow for feeding. *Active* suspension feeders use cilia or muscles for pumping water past the filtering surface. This feeding may be augmented by the ambient velocity, which can be an order of magnitude greater than the self-generated currents (Merz, 1984; Okamura, 1984, 1987).

Recently a few studies have begun to examine and clarify particle capture mechanisms in biological systems. Particle size selection has been shown to depend on the diameter and spacing of the filtering elements, flow velocity past the elements, diameter of the particles, and surface chemistry of both particles and filtering elements (Rubenstein and Koehl, 1977; LaBarbera, 1978, 1984; Gerritsen and Porter, 1982). However, the most broad-scale aspects of filter feeding are still poorly understood, especially the functional role of overall organismal design in maintaining the organism's exposure to flow and in influencing the hydromechanical conditions which aid in particle capture. In some stony corals the branching pattern prevents the formation of stagnant zones within the colony. This assures adequate flow throughout (Chamberlain and Graus, 1975). In flexible organisms, their shape and exposure to flow depend on the flow velocity and the structure's response to drag forces imposed by the flow (Koehl, 1976; Patterson, 1984; Vogel, 1984), thereby changing the microenvironment around the filtering elements (Harvell and LaBarbera, 1985).

The present study emphasizes the effect of gross morphology on feeding performance in a particular suspension feeder to highlight the potential interactions between morphology and flow which may occur in a wide range of suspension feeders. The ecological consequence

of functional morphology is equated with "feeding rate" which is defined as the total number of particles caught per unit time. In this analysis, feeding rate is a function of three parameters: (1) the volume of water processed by the organism per unit time, (2) the proportion of particles removed per volume of water processed, (3) and the density of particles in the ambient water. The first two factors, the "accessibility" to flow and the "filtering efficiency" or proportion of particles retained, may both be influenced by the ambient velocity. For a benthic organism, several factors may affect the ambient velocity it experiences, including its own size and height above the substratum into the boundary layer (Nowell and Jumars, 1984).

This paper first describes an approach for examining the effect of structure-flow interactions on feeding. It then describes a series of field and laboratory studies of feeding rate in a passive suspension feeder which address these questions: (1) how does ambient flow speed independently affect volume flow rate and filtering efficiency, two components of feeding rate? (2) How are volume flow rates and filtering efficiency affected by organism size, as the organism grows and extends into a different ambient flow environment? (3) How does the structural response of the organism to ambient flow influence particle capture on the level of the filtering elements, or polyps?

Integrative analysis of suspension feeding

An approach useful for evaluating the effect of morphological features on the feeding rate of passive suspension feeders is presented. I first identify parameters (environmental and morphological) which may influence feeding and then define the relationships of these parameters. For example, an analysis of feeding mechanics encompasses several aspects of structural design which emphasize the interaction between animal structure and ambient flow:

(1) *Structural features related to maintaining filter surface area exposed to the flow.* Drag imposed by the flow will tend to deform flexible organisms. In organisms which require flow *through* the filter for feeding, it is the drag-induced pressure drop across the filter that drives the water through the filter; hence, the organism cannot "hide" from the flow and must have support structures to maintain the filter in the flow. In organisms which utilize flow over or around the filter, such as in gravitational deposition feeders, filter surface area or position in flow must be maintained.

(2) *Structural features which stabilize the filter in relation to changes in flow direction or amplitude.* For short-term fluctuations in current speed or direction, on the

order of seconds to hours, the animal may stabilize the filter either by actively or passively re-orienting, and thus ensure proper exposure. For long-term fluctuation, from days to years, re-orientation and stabilization may occur via growth responses (*e.g.*, Wainwright and Dillon, 1969).

(3) *Flow-structure interactions related to particle capture.* Large scale features may pre-position particles before they contact the filter (Craig and Chance, 1981), or pre-condition the water and its flow characteristics, such as flow speed, through the filter (Harvell and LaBarbera, 1985).

The design aspects listed above all influence feeding. The first two aspects influence the volume of water processed by the organism and the last influences filtering efficiency. The total number of particles extracted per unit time is a function of the volume of water processed per unit time, the number of particles in the ambient water, and the proportion of particles removed per unit volume of water processed, and can be expressed as the equations given in Figure 1.

Structural and flow features can be identified which may affect either "accessibility" or "filtering efficiency" (refer to Fig. 1). For example, filtering efficiency depends on the flow pattern and particle paths around the filtering elements, and thus is a function of flow velocity around the elements; the size, spacing, orientation, and surface charge of elements; the diameter, density, motility, and surface charge of the particles; and possibly the frequency with which the elements are cleaned (Fuchs, 1964; Rubenstein and Koehl, 1977; Spielman, 1977; LaBarbera, 1978, 1984; Gudmundsson, 1981).

"Accessibility" can refer to the volume of water passing either through a filter or in close enough proximity that particle extraction is possible. In organisms where the flow is quasi-perpendicular to the filter, as in the sea pen *Ptilosarcus gurneyi*, access to flow is equated with volume flow rate. It is equal to the surface area of the filter exposed to the flow times the velocity of flow through that area (refer to Fig. 1). The surface area of the filter exposed to the flow is a function of the organism's vertical stance and orientation to the flow; the shape, size, and flexibility of the filter; the ambient velocity and the drag imposed by the flow; the position of the organism above the substratum and the presence of other organisms. The influence of most of these parameters on accessibility in the suspension feeding sea pen *Ptilosarcus gurneyi* is addressed in Best (1985, in prep.).

Having identified both flow characteristics and morphological features which may affect feeding rate, I examined the influence of flow velocity on both volume flow rate and filtering efficiency, with particular attention
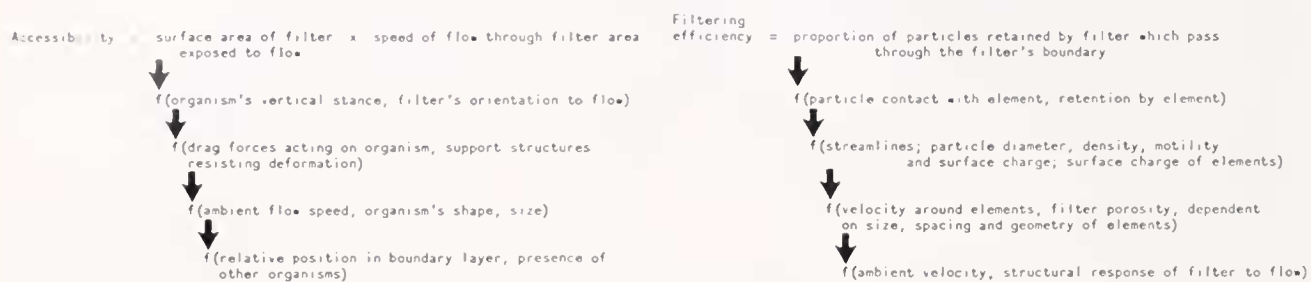
Figure 1. Diagram of integrative method, showing relationships among parameters. See text for discussion.

to flow-structure interactions that change with ambient flow speed.

Materials and Methods

Experimental organism and morphology

The sea pen *Ptilosarcus gurneyi* (Cnidaria: Pennatulacea) was used in this study because it has a well-defined morphology which can be easily characterized on the basis of size and age (Birkeland, 1969, 1974). The upper portion of the organism, the rachis, contains the filtering elements—the polyps—which extend from the semi-circular horizontal plates termed "leaves" (Fig. 2). With an increase in ambient velocity, the flexible rachis bends downstream (Fig. 2). The polyps form a semi-cylindrical filter on the downstream side of the organism, extending the length of the rachis (Fig. 2). The height (vertical stance) of the rachis was the indicator of organism size. The rachis behaves as a single unit which orients to the flow (Best, 1985), ensuring water passage through the filter in the same direction—into the concave side of the semi-cylindrical filter. This sea pen feeds primarily on phytoplankton (Birkeland, 1969). Its bright orange color is the result of carotenoids incorporated from ingested dinoflagellates and can be passed on to the tissues of nudibranch predators (S. Kemp, pers. comm.).

Ptilosarcus gurneyi is a common inhabitant of soft-sediment environments in Puget Sound and the San Juan Archipelago. Washington. From an initial length of under 1 mm, *P. gurneyi* can grow to a total length of over 80 cm, extending over 40 cm above the benthic surface. Sea pens were hand collected from Lopez Sound by SCUBA diving and transported back to the Friday Har-

bor Laboratories of the University of Washington. Animals were maintained in running seawater.

Morphometrics

Photographs of organisms in the field were compared to photographs of fully expanded organisms in the laboratory. Since there were no differences detected in stance or body size between laboratory and field photographs, all morphometrics were performed in the laboratory. With a Wild dissecting microscope, polyp sizes in small (3–10 cm rachis height) and large (20–30 cm rachis height) sea pens were measured. For each organism, polyp width, tentacle width and length, and pinnule length and spacing were measured to the nearest 0.01 mm. Polyps from the bottom, middle, and top of the rachis from each sea pen were examined.

Sea pens were placed in a large recirculating flow tank (working area of 32 by 34 cm; Vogel and LaBarbera, 1978), continuously supplied with fresh seawater. To examine spacing between polyps as a function of flow speed, close-up photographs of the sea pens were taken as they deformed under flow speeds up to 25 cm s^{-1}. From these photographs, the spacing between the leaves and the density of polyps were determined. Polyp density was calculated as the number of polyps cm^{-2} in the plane of the filter, approximating a plane perpendicular to the direction of flow.

Field velocities

Sea pens were studied within Lopez Sound where water depth averaged 10 m and the bottom consists of sandy-mud. To characterize the flow environment on the
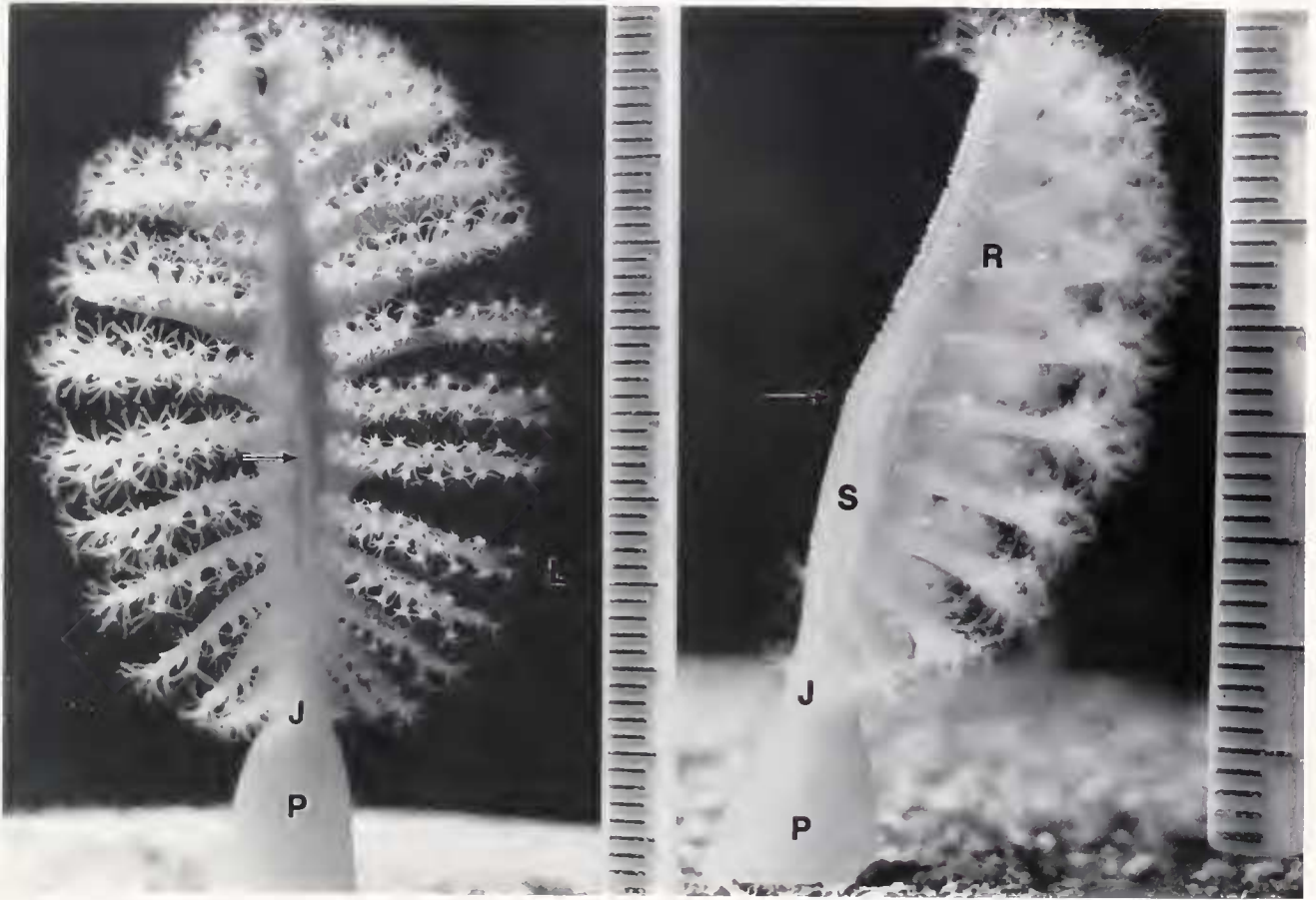
Figure 2. Photographs of small sea pens, *Ptilosarcus gurneyi*. Left. View of sea pen showing the array of polyps on the downstream side of the rachis (rachis height = 4.5 cm), "J" - Joint, "P" - Peduncle, "L" - Leaf. Arrow points to internal style visible through body wall. Note the parallel leaves "L" through which water would flow. Right. Side view of sea pen (rachis height = 3.0 cm), "P" - Peduncle, "J" - Joint, "S" - Siphonozooids, "R" - Rachis. Arrow points to the top rigid portion of the style. Flow is from left to right.

scale of the sea pens, a thermistor flow probe (LaBarbera and Vogel, 1976) was used to record local flow speeds at 18 cm above the substratum, the average height of the sea pens. Flow direction was also continuously monitored with a weather vane/potentiometer (Best, 1985). Velocity recordings were made over 6–8 hour periods, including one low and high tide, on three different days. To construct a velocity profile and determine the range of velocities experienced by small, medium, and large sea pens, velocity measurements were taken at different heights above the substratum.

Volume flow rates

There is a postural change in *Ptilosarcus gurneyi* with increasing flow speed. The area of the feeding filter oriented perpendicular to the current also changes with the flow speed. Therefore, it was necessary to measure di-

rectly the volume flow rate through the filter as a function of ambient flow speed.

Sea pens acclimated in the recirculating flow tank. An imaginary plane was established upstream of the organism and horizontal transects across this plane were made with a fluorescein dye injector. For each horizontal transect, it was noted for which points the dye, once released, subsequently passed through the filter of the downstream sea pen. Horizontal transects were spaced vertically every 1.0 cm for large and medium sea pens and 0.5 cm for small pens. From these transects an area on the imaginary plane was determined, representing the source of water actually passing through the filter. The volume flow rate was calculated by multiplying this area by the water flow speed through the plane (area $\times$ speed = volume time^{-1}). Flow speeds in the flow tank were measured with a thermistor flowmeter which had been calibrated with an electromagnetic water current meter

(Model 511. Marsh-McB[?]rr[?] Inc., with a precision ± 2[?]).

For each sea p[?] flow rates were determined over a range o[?] [?]ls. 1 to 25 cm s⁻¹ for medium and large pen[?] [?] to 12 cm s⁻¹ for small pens. Determinations of [?] flow rates were repeated three times for a large [?] small sea pen; replicated values were within 3[?] for the small sea pen and less than 6% for the large sea pen.

Velocity through rachis

A thermistor flow probe measured the flow speed between the leaves and through the mesh-work of polyps as sea pens were exposed to ambient speeds of 1 to 25 cm s⁻¹ in the flow tank.

Filtering efficiency

In the field, water samples were collected upstream and downstream of sea pens from three size classes: a small sea pen with a rachis height of 7 cm, medium sea pen 15 cm high, and large sea pen 25 cm high. For each sea pen three concurrent upstream-downstream water samples were taken by SCUBA divers positioned on either side of the organism. Each diver held a transparent plastic tube, parallel to the current, either directly in front of the rachis or directly behind the rachis, at the same height. The tubes were held in place long enough to be flushed with seawater several times. Simultaneously, the ends of both tubes were sealed. Three sized tubes were used for the different sized sea pens, with 3 cm, 5 cm, and 7 cm diameters, respectively.

Upon leaving the water, the divers transferred the water samples into clean bottles, stored them on ice in the dark, and immediately took them to the laboratory for analysis.

In the laboratory each water sample was first filtered through a 163 μm Nitex filter. An Elzone 80XY particle counter (Particle Data, Inc.) was used to count the total number of particles in a 2 ml subsample, and to construct a size-frequency distribution of the particles into 128 particle size classes in the range 0–100 μm. Five subsamples were analyzed from each upstream and downstream field sample. The precision of counts from multiple subsamples is better than 5%.

To examine the effect of flow speed on particle retention, a laboratory experiment was conducted involving a medium-sized sea pen (rachis height [?] 12 cm). The sea pen was allowed to acclimate in the recirculating flow tank. A filtrate of natural particles—containing phytoplankton and particulates ranging from 1–80 μm in diameter—was added to the flow tank. A density between 3000–4000 particles ml[?] was maintained throughout the experiment. At each of three flow speeds, 1.5, 3.0, and 6.0 cm s⁻¹, water samples (40–70 ml) were collected concurrently with a suction device (5 mm diameter opening) immediately upstream and downstream of the rachis. Three sets of water samples were taken at each velocity.

In addition, experiments similar to the above were conducted with a medium sea pen feeding on one size range of particles, by adding only the chlorophycean phytoplankter *Dunaliella* (10 μm diameter) to the flow-tank. The water samples from the laboratory experiments were treated and analyzed for particle counts in the same manner as in the field experiment, but with 1 ml subsamples.

Filtering efficiency was calculated from the difference in particle counts from two samples, taken concurrently up- and downstream, and expressed as a percentage of the upstream count.

Results

Field velocities

Flows at the field site were relatively steady, hydraulically smooth and bidirectional, and changed orientation approximately 180° with the tides. The mean flow speed at 18 cm above the substratum ranged from 8 to 11 cm s⁻¹. The maximum speeds ranged from 13 to 17 cm s⁻¹. Over a 10 minute period, for a mean flow speed of 9.8 ± 0.42 cm s⁻¹, the turbulence intensity (standard deviation of the flow/mean flow speed) was 0.043. At 8 cm above the sediment—the approximate height of small sea pens—the mean flow speed ranged from 3 to 7 cm s⁻¹ and the maximum speeds ranged from 8 to 10 cm s⁻¹. Velocity readings taken over a few minutes at 5, 10, 30, 50, and 100 cm above the substratum showed mean flow speeds of 6.5, 7.7, 8.7, 9.6, and 10.2 cm s⁻¹, respectively. Using the standard log layer equations for a geophysical boundary layer and the linear regression of the above means, the boundary shear velocity (u_*)—a measure of shear stress acting on the bed and a useful parameter of the flow field—was estimated to be 0.50 cm s⁻¹.

Morphometrics

Polyp width, the distance across the polyp between tentacle tips, is uniform throughout large sea pens and the middle and bottom regions of small sea pens (3.59 mm ± 0.157, n = 25). The very top 30–40 polyps on the small sea pens are slightly larger with a mean width of 3.88 mm ± 0.217 (Student's t-test, $t = 2.34$, $α = 0.05$, n = 30). Tentacle length ranged from 1.4 to 1.9 mm, with a mean of 1.59 mm ± 0.13 (n = 30). The tentacle width was approximately 0.34 mm at its base and tapers to the
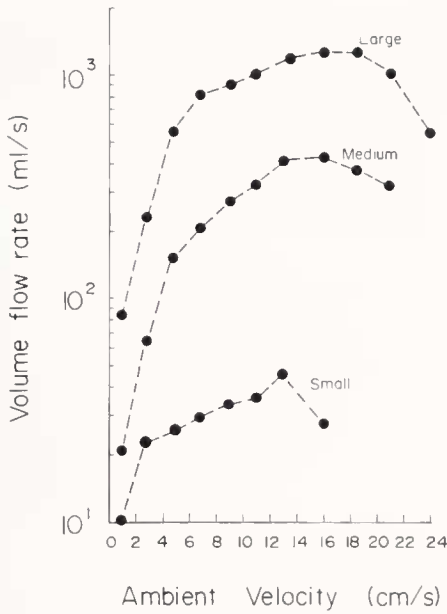
Figure 3. Volume flow rate as a function of ambient velocity. The volume of water passing through the rachis initially increases as velocity rises, then peaks and declines due to the postural change of a sea pen.

tip. Eleven to twelve pairs of pinnules project out along the length of the tentacle, increasing from a length of 0.07 mm at the tentacle base to 0.32 mm at the tentacle tip. These pinnules do not project laterally out from the tentacle, but are angled downstream. Pinnule width ranged from 0.03 to 0.05 mm. Spacing between pinnules ranged from 0.06 to 0.13 mm.

The spacing between the leaves, on the downstream side of the animal, was smaller in the small sea pens (3.8 mm mean spacing, 3.1–4.2 range, n = 6 organisms) than in the large sea pens (5.7 mm mean, 5.4–5.9 range, n = 7) in still water. With increasing flow speeds both small and large sea pens flex with the flow, resulting in a decreased spacing between leaves. At 13 cm s^{-1}, small sea pens had a mean spacing of 2.3 mm, range 2.6–2.8; large sea pens had a mean spacing of 3.9 mm, range 3.5–4.2. At 20 cm s^{-1}, large sea pens had a mean of 3.4 mm, range 3.2–3.6.

In still water polyp density, in the plane of the filter, is 30.2 ± 1.76 polyps cm^{-2} (n = 12) in large sea pens and 29.4 ± 2.35 polyps cm^{-2} (n = 12) in small sea pens. As ambient flow speed increases to 13 cm s^{-1}, polyp density does not change significantly in small sea pens. However, in large sea pens there is a significant increase in polyp density to 33.1 ± 0.13 polyps cm^{-2} (Student's t-test, t = 3.58, α = 0.05, n = 24).

Volume flow rates

The volume of water flowing through the filter per unit time (volume flow rate) is dependent on both the ambi-

ent flow speed and the area of filter projected into the flow as determined by the posture of the organism (Best, 1985). As shown in Figure 3, the volume flow rate for a single organism increases with an increase in ambient flow until the organism becomes so bent back by the flow that more water tends to flow over rather than through the filter. The maximum volume flow rate, y (ml s^{-1}), attained for an organism is best fit by a linear function (stepwise multiple regression analysis) of its rachis height, χ (cm), where

$$y = -208.4 + 54.6\chi \quad (r = 0.93, n = 18).$$

The flow speeds at which these maximum volume flow rates occur are also related to the organism's size. For small sea pens, the maximum volume flow rates occur at flow speeds ranging between 6.5 and 8.5 cm s^{-1}, between 12 and 14 cm s^{-1} for medium sea pens, and between 14 and 18 cm s^{-1} for large sea pens.

Velocity through rachis and Reynolds number

Figure 4 shows the flow speed between the leaves and directly behind the polyps in relation to the ambient flow speed. As the ambient speed increases, the flow speed between the leaves and polyps also increases, but at a lower rate (slope of regression lines less than 1.0: for leaves, b = 0.55, t_s = 8.58, $t_{.05[6]}$ = 2.31, $P < 0.05$; for polyps, b = 0.33, t_s = 26.78, $t_{.05[6]}$ = 2.31, $P < 0.05$). At an ambient speed of 25 cm s^{-1}, the flow speed between the polyps is only 6–8 cm s^{-1}, and 11–13 cm s^{-1} between the leaves.

For an object moving relative to the ambient fluid, the relative importance of inertial and viscous forces acting on the object—and therefore the nature of flow around the object—is represented by the dimensionless parame-
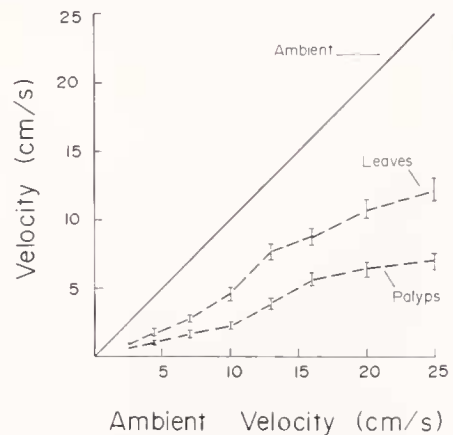

Figure 4. Flow velocities between leaves and behind the polyps as a function of ambient velocity. Note the much reduced flows occurring by the polyps.
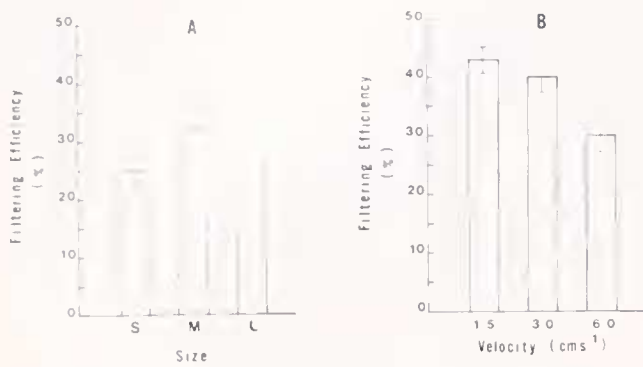
Figure 5. A. Filtering efficiency as a function of organism size. Filtering efficiency is calculated as the percentage difference in particle counts from upstream and downstream water samples taken in the field. Means ± SE are shown for 15 paired water samples (2 ml) analyzed for each small "S", medium "M", and large "L" sea pen. Field flow speeds for the small sea pen were approximately 5–6 cms⁻¹ and 8–9 cms⁻¹ for the medium and large sea pens. Particle retention in the small sea pen is significantly lower than the medium and large sea pens (2 × 2 G-test of independence, G = 56.6, α = 0.05) B. Filtering efficiency as a function of ambient flow speed. Filtering efficiency for a single sea pen feeding in the flow tank at three different speeds. Means ± SE are shown for 15 paired water samples (1 ml). Particle retention decreases with increasing velocity (ANOVA, $F_{2,44}$ = 75.52, P ≪ .001, n = 45).

ter "Reynolds number" (Re). For medium and large sea pens, assuming the characteristic length to be the length of the rachis parallel to flow, the Reynolds number is around 8×10^2 to 1×10^4 for flows from 2 to 25 cm s⁻¹; for small sea pens the Reynolds number is around 2×10^2 to 3×10^3. However, due to the small size of the pinnules and tentacles (i.e., small characteristic length) and the reduced flows over these structures, the nature of the flow is very different as reflected in the Reynolds number (Re: approximately 1–10 for tentacles, and 0.1–1.0 for the pinnules). Particle capture is occurring under low Reynolds number, viscous flow conditions.

Filtering efficiency

Figure 5A shows the filtering efficiencies—the percentage of particles present in the downstream water sample relative to the upstream sample—for the three different sized sea pens in the field. The small sea pen had the lowest retention of particles which was significantly different from the higher retentions of the medium and large sea pens (2 × 2 G-test of independence performed on raw particle counts, G = 56.6, α = 0.05). The relationship of filtering efficiency to ambient flow speed for one sea pen is shown in Figure 5B, the efficiency decreased from a mean of 42.8% ± 3.5% at a velocity of 1.5 cm s⁻¹ to a mean of 29.9% ± 5.1% at a velocity of 6.0 cm s⁻¹. An ANOVA failed to show a significant difference in the

number of particles in the upstream samples throughout the experiment ($F_{2,44}$ = 1.62, P > 0.21, n = 45), but did show a significant interaction between ambient flow speed and the number of particles in the downstream samples ($F_{2,44}$ = 75.52, P ≪ .001, n = 45). Filtering efficiency decreases with increasing velocity.

The size-frequency distribution of particles in one set of upstream-downstream water samples taken in the field is shown in Figure 6; the difference between the area under these two curves represents the number of particles removed during one passage through the rachis. Every field feeding test failed to show a significant difference in the size-frequency distributions of the upstream-downstream water samples (G-test for goodness of fit), implying that no particle size selection was occurring. However, for the laboratory feeding experiments, there were significant differences (G-test for goodness of fit) in the size-frequency distributions of every upstream-downstream comparison (Table 1). The mean particle size in the downstream sample was smaller than that for the upstream sample, implying that larger particles had a higher probability of being retained. The difference between the mean particle size of upstream-downstream samples increased as ambient flow speed increased (Table 1), suggesting a greater selection for larger particles at higher ambient flow speeds.

Feeding performance

The total number of particles removed from the ambient water per unit time, the feeding rate, is equal to the product of volume flow rate and filtering efficiency. Feeding rates, calculated from these two independently measured parameters, of a large, medium, and small sea pen are shown in Figure 7, assuming an ambient particle concentration of 1000 particles ml⁻¹ which is within the range of concentrations present in the field. Because filtering efficiencies were only measured for flow speeds up
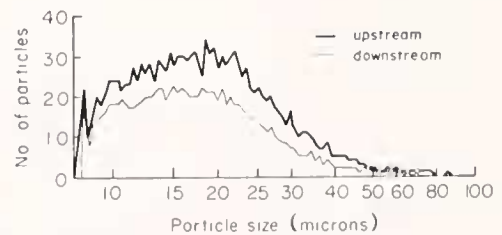

Figure 6. Size-frequency distribution of one set of upstream-downstream water samples from the field for a 15 cm sea pen in 6 cm s⁻¹ flow. The total number of particles in 1 ml subsamples are shown. Note the similarity in curves; the size-frequency distributions are not significantly different (G-test for goodness of fit, G = 80.5, $\chi^2_{05[71]}$ = 93.9, P > 0.1).

Table I

Laboratory feeding experiments: differences in particle size distributions between paired upstream-downstream water samples

Ambient flow speed	Mean particle size (μm)		
	Up	Down	G-test
1.0 cm s^{-1}	9.6	9.6	95.6*
	10.1	9.7	219.0*
	10.3	9.7	168.4*
	$\bar{x} = 10.0$	9.7	
3.0 cm s^{-1}	10.1	9.6	195.6*
	10.3	9.6	231.2*
	10.3	9.9	377.8*
	$\bar{x} = 10.2$	9.7	
6.0 cm s^{-1}	10.4	10.0	146.1*
	10.2	9.9	145.1*
	10.6	9.9	276.5*
	$\bar{x} = 10.5$	9.9	

Means for each water sample are based on a count of 10,000 particles from natural filtrate. G-test for goodness of fit used to compare frequency distribution of 75 particle size classes (1–100 μm) of upstream and downstream water samples. G-test, $\chi^2_{05[73]} = 93.9$, * significant at $\alpha = 0.05$.

around the polyps, coupled with polyp density, influence the size range of particles retained by the filter.

Size, flexibility, and volume flow rate

In many benthic communities, occupation of space above the substratum is at a premium (Jackson and Buss, 1975; Jackson, 1977; Sutherland and Karlson, 1977). Access to flow for these benthic organisms will depend on their protrusion above the substratum and the projected area of the filtering appendages relative to the flow direction. Volume flow rates are dependent on ambient flow speed and filter size, both of which increase as the organism grows. Volume flow rate refers to the volume of water which passes through the filter "boundary" of an organism per unit time.

For a sea pen, the volume flow rates initially increase with increasing flow speed, but then peak and decline due to deformation of the organism. The maximum volume flow rate and the ambient velocity at which it occurs are both dependent on organism size. As the animal bends in the flow, more water passes over it rather than
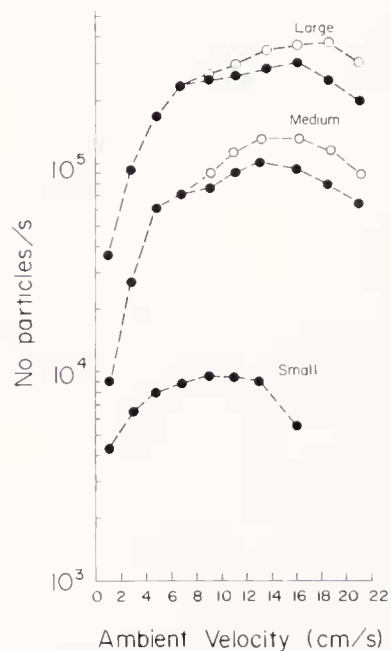
to 6 cm s^{-1} in the laboratory, filtering efficiency values for higher flow speeds were estimated to decrease to 20% in the absence of rachis deformation (closed circles). From the field experiments, efficiencies are known to remain around 30% (represented by open circles), probably due to a decrease in filter porosity as the rachis bends downstream. Feeding rate is largely determined by volume flow rate (compare Fig. 7 with Fig. 3); with increasing flow speed feeding initially increases, peaks, then decreases.

Discussion

Structure-flow interactions

Structure-flow interactions are important to suspension feeders which depend on relative movement of food particles past a filtering structure. (1) In flexible organisms, the drag forces on the organism will change the shape and vertical stance of the filter. These drag forces are dependent on the filter shape, size, orientation, and flexibility. The absolute (rachis height) and relative (degree of bending) vertical stance of the filter determine the volume of water flowing through the filter. (2) Flexibility regulates the speed and pattern of the flow past the filtering structures, and thus filtering efficiency. Efficiency depends on the packing array and density of polyps, which can change with ambient velocity. (3) Flow patterns

Figure 7. Feeding rate as a function of flow speed and rachis deformation. Using the determinations of volume flow rate and filtering efficiency, feeding rates of a large (rachis = 24 cm), medium (rachis = 15 cm), and small (rachis = 8 cm) sea pen are shown. Open circles represent feeding rates calculated using 30% efficiency at the higher flow speeds, as recorded in the field for medium and large sea pens; closed circles beneath the open circles represent feeding rates assuming that efficiency would continue to decrease to 20% at the higher flow speeds in the absence of rachis deformation.

through the rachis. Rachis flexibility prevents drag from rising exponentially (Best, in prep.), maintains lower velocities through the filter and past the polyps, and changes the porosity (polyp density) of the filter. Parameters influencing vertical distance—such as filter shape and size, drag, and structures resisting drag, are discussed in detail in Best (in prep.).

Ambient velocity, filter porosity, and filtering efficiency

Filtering efficiency, in engineering vernacular, is defined as the number of particles contacting a fiber relative to the number of particles which would have passed through the fiber area had the fiber not been there to divert streamlines (Fuchs, 1964; Spielman, 1977). Most biological filters are a composite of fibers of various dimensions and configurations that can change with organism growth and ambient flow. A more usable definition of efficiency for biological filters is the proportion of particles retained from a given volume of water within an organism's "access" to flow. For filters perpendicular to steady flows, access is the volume of water which passes through the filter's boundary. For filters perpendicular to oscillating flows or oriented parallel to flows, access is the volume of water passing sufficiently close to the filter from which particles *may* be extracted. Filtering efficiency depends on the position of fluid streamlines around the filtering elements and the particle paths around the filtering elements.

Rubenstein and Koehl (1977) were the first to compare filtering structures of aquatic organisms to manmade aerosol filters that have the potential of capturing particles by a number of non-sieving mechanisms (*e.g.*, Fuchs, 1964). Spielman (1977) extended the engineering analysis of particle capture by filters in aqueous media, leading to predictive models of the mechanisms, nature, and size of particles captured by these filters. The primary mechanism of particle capture for many biological filters appears to be by direct interception, aided possibly by electrostatic or London-van der Waals forces (for review see LaBarbera, 1984). This mechanism has been used to explain particle capture by brittle stars (LaBarbera, 1978), crinoids (Meyer, 1979), aquatic insects (Craig and Chance, 1981; Silvester, 1983), and cnidarians (Koehl, 1977; Patterson, 1984). As originally developed for airborne particles, capture by direct interception assumes that the center of a neutrally buoyant particle follows an undisturbed streamline around a filtering fiber; if the streamline and the center of the particle pass within one particle radius of a fiber, contact occurs and the particle is retained. As a *waterborne* particle approaches a fiber, it must deviate from the undisturbed streamline due to the slow drainage of fluid from the gap

between the surfaces as the particle and fiber approach (Spielman, 1977). For contact to occur in aqueous media, the action of attractive forces (electrostatic or van der Waals forces) must be invoked to overcome the slow, viscous drainage. If the center of the particle passes within some critical distance, the attractive forces will be sufficient to insure contact with the fiber (Spielman, 1977). These models apply to single fibers and assume that all particles contacting the fiber remain caught.

In a test of Spielman's theories, LaBarbera (1984) found relatively good agreement between the predicted and actual size distribution of Sephadex beads (40–360 μm) caught by the brittle star *Ophiopholis aculeata*. Disagreements between observed and predicted distributions may be due to two factors. First, the model assumes a single filtering fiber, but brittle stars use an array of pinnules, resulting in flow interaction and changes in the direction of streamlines (Fuchs, 1964). Second, it is assumed that all particles contacting the fiber remain caught; this assumption has not been tested for a biological filter, especially when large active particles, such as zooplankton, are caught.

Direct interception is inversely dependent on flow velocity (Spielman, 1977). Contrary to the volume flow rate, filtering efficiency decreases with an increase in ambient flow speed, as shown in the laboratory experiment. In this laboratory experiment, I used a maximum flow speed of 6.0 cm s^{-1}. At speeds faster than this, the sea pen in the flow tank would begin to bend back significantly, increasing polyp density, and thus altering the geometry of the filter by compressing the polyps closer together. The laboratory experiment showed that, for a given porosity filter, a decrease in particle retention occurs with increasing ambient velocity.

The filtering network of *Ptilosarcus gurneyi* is not strictly two-dimensional. Water entering the rachis first passes between the leaves, and a velocity profile is established with the faster flow down the middle. On the downstream edge of the organism, the polyps extend between the leaves into the faster flow. The polyps, and their tentacles and pinnules, are oriented slightly downstream in such a way that they continually bisect the velocity distribution. In this way, the filtering elements are placed in the regions of "unfiltered" water, increasing the probability of particle contact.

In the field experiments, it was found that the medium and large sea pens had higher filtration efficiencies than the small sea pen, even though they were exposed to higher ambient flow speeds above the substratum. Under ambient flow, polyp density is higher in the larger sea pens, resulting in a lower "porosity" or spacing between the polyps. A lower filter porosity would increase the total filtering surface in a given volume, reduce the velocity

profile between neighboring filtering elements, and decrease the distance between particle streamlines and the element's surface. As ambient flow speed increased, sea pens are bent back by the flow, compressing the downstream array of polyps and decreasing porosity further. Structure-flow interactions therefore result in a "variable porosity filter" which can maintain a higher efficiency at higher ambient flow speeds.

Particle size selection

A review of Figure 6 reveals that, overall, the size distribution of particles retained follows closely the size distribution in ambient water. In fact, in the feeding experiments conducted in the field, there was no difference between upstream and downstream water samples in size distribution of particles. There was a difference detected in the laboratory experiments, perhaps because of the higher particle counts used to construct the distributions (10,000 particles in laboratory experiments *versus* 1500–3000 particles in field experiments). Although there was a preference towards the retention of larger particles in the laboratory experiments here and in LaBarbera's (1984) study with brittle stars, the distribution of particles retained still closely follows the availability of particles. There is no steep demarcation or stepped character in the distribution. Due to the mechanisms of particle capture operating in aqueous media, and the abundance of small particles in natural seawater (McCave, 1984), a high degree of selectivity for large particle sizes, to the exclusion of small particles, appears to be precluded. Whether or not an organism feeds on the small particles of detritus and phytoplankton in the sea, its filter will tend to collect these particles.

Feeding performance

Feeding performance is dependent on flow velocity in bryozoans (Okamura, 1984, 1985) and octocorals (Leversee, 1976; Patterson, 1984), and on swimming speed in juvenile fish (Friedland *et al.*, 1984). In the flexible bryozoans and octocorals studied, colony shape changed with ambient velocity; bryozoan branches collapsed inward and downstream (Okamura, 1984), while in octocorals individual polyps bent downstream (Patterson, 1984). These structural changes can influence feeding performance by altering both volume flow rate and filtering efficiency—two parameters influenced by ambient velocity and resulting structure-flow interactions. In this study I examined these two parameters independently. Feeding rate in the sea pen *Ptilosarcus gurneyi* is highly dependent on volume flow rate. Both feeding rate and volume flow rate initially increase sharply as flow speed increases, and then decrease as the upright posture de-

creases. Small sea pens have a lower feeding rate because of lower volume flow rates, due to smaller filters and lower ambient flow speeds near the substratum in the boundary layer. Filtering efficiency decreases with increasing flow speed, which may be compensated for by a change in filter porosity; polyps become more closely packed as flow speed increases.

Because feeding rate is dependent on a complex interplay of volume flow rates, filtering efficiencies, organism size and flexibility, and ambient velocity, competitive feeding interactions between organisms may be due not only to direct reduction of resource supplies, but may also be mediated by altering the ambient velocity. In the arborescent bryozoan *Bugula stolonifera*, Okamura (1984) found that feeding success in small colonies was reduced by both fast ambient flows and the presence of a large colony upstream. In the first case, fast ambient flows may have resulted in lower volume flow rates or reduced efficiencies. In the second case, the larger colony upstream may have depleted particles in the ambient water, or restricted the volume of water passing through the smaller colony.

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